Madroño, Vol. 57, No. 4, pp. 220–228, 2010

PLANT POPULATION AND HABITAT CHARACTERISTICS OF THE ENDEMIC SONORAN DESERT CACTUS *PENIOCEREUS STRIATUS* IN ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA

Greta Anderson
School of Geography and Development, University of Arizona, P.O. Box 210076, Tucson, AZ 85721

Sue Rutman
National Park Service, Organ Pipe Cactus National Monument, 10 Organ Pipe Drive, Ajo, AZ 85321

Seth M. Munson[1]
U.S. Geological Survey, Southwest Biological Science Center, Canyonlands Research Station, 2290 S. West Resource Blvd., Moab, UT 84532

Abstract

Peniocereus striatus (Brandegee) Buxb. (Cactaceae) is an endemic Sonoran Desert cactus that reaches its northern range limit in southwestern Arizona. One U.S. population occupies a small area of Organ Pipe Cactus National Monument near the U.S./Mexico international boundary, which has been monitored since 1939. An extensive survey conducted in 2002, covering 177 ha, resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in previous surveys. Despite potential increases in population size and spatial distribution, mean plant height and number of basal stems has not significantly changed in recent years. Bud scars revealed that a majority of the population was sexually mature. *Peniocereus striatus* occurrence increased with decreasing slope, spanned every slope aspect, and was highest on rocky soils, but was noticeably low on west and northwest slopes and areas where severe land degradation had previously occurred. Over half of *P. striatus* plants were nursed by shrubs and subshrubs, while 40% occurred under leguminous trees. A severe frost in January 2002 top-killed 19% of the population, with the greatest damage in drainage bottoms. However, long-term (1944–2002) climate records show that there has been an overall increase in the number of frost free days in the region, which, coupled with land use change, has implications for the future health of this population.

Key Words: Cardoncillo, climate, frost-tolerance, gearstem cactus, habitat suitability, land use history, night-blooming cereus, nurse plant.

The small population sizes, narrow geographic ranges, and high habitat specificity make rare endemic plant species particularly vulnerable to accelerated climate and land use changes (Rabinowitz 1981; Malcolm et al. 2006). The viability and persistence of rare endemic plants depends on the maintenance of suitable habitat and the ability of the population to propagate itself under changing environmental conditions. In the Sonoran Desert, several endemic plants, including cacti, are of tropical descent and known to be limited in their northern distribution by freezing temperatures (Shreve 1911; Hastings 1963). Anthropogenic global warming is likely to decrease the intensity and frequency of freezing temperatures, which may create opportunity for expansion of frost-intolerant plant species (Lyford et al. 2003). In addition to climate, Sonoran Desert endemic plants are likely to respond to changes in land use that occur in their local habitat, including livestock grazing, wood harvesting, cropping practices, and other activities (Suzán et al. 1994). Close study and monitoring of plant populations and their habitat at the periphery of their geographic ranges can contribute to an understanding of the factors that limit their distribution, provide information on the sustainability of the population, and help inform conservation strategies.

Peniocereus striatus (Brandegee) Buxb. is a slender-stemmed cactus endemic to frost-free areas of the Sonoran Desert (Felger 2000). This inconspicuous sub-erect to sprawling, vine-like cactus is typically 25–75 cm tall (Pinkava 1995) and up to 2 m tall in some microhabitats (Felger 2000). *Peniocereus striatus* has small, scattered populations throughout Mexico (Baja California, Sonora, and Sinaloa) and is very rare in the U.S., where it reaches its northern range limit in southwestern Arizona (Benson 1982; Nabhan 1992; and Felger 2000). One of the few *P. striatus* populations in the U.S. occurs in a small area of Organ Pipe Cactus National Monument

[1] Corresponding author: SMunson@usgs.gov

(OPCNM) near the U.S./Mexico international boundary. This population was first recorded from Gray's Well in 1939 (OPCNM Herbarium, NE of Sonoyta, 20 April 1939, *A.A. Nichol s.n.*), and no other population has been reported from any other area in OPCNM.

Past research has found that populations of *P. striatus* have higher densities and larger plant sizes south of OPCNM at less disturbed sites (Suzán et al. 1994). The condition of *P. striatus* improves under perennial nurse plants, which modify the environment by buffering extreme temperatures, increasing water and nitrogen availability, reducing photosynthetically active radiation, providing physical support and protection from herbivores (Franco and Nobel 1989; Suzán et al. 1996). Recruitment of *P. striatus* is low, most likely because it has few species of pollinators, blooms nocturnally during a few episodes, and has low floral and fruit production (Benson 1950; Suzán et al. 1994; Raguso et al. 2003).

Previous reports suggested that *P. striatus* in OPCNM occurred more frequently on rocky hill slope habitat (Jackson 1966; Steenbergh 1966; Suzán et al. 1994; Goodsell unpublished), which contrasts with observations that *P. striatus* in Mexico prefers flat sites more than rocky slopes (T. Van Devender and M. Dimmitt, Arizona-Sonora Desert Museum, personal communication; G. Anderson and S. Rutman personal observation). We hypothesize that *P. striatus* occurred on rocky hill slopes in OPCNM during a historical period of high land use intensity because these sites provided refugia from plant mortality and habitat degradation associated with livestock grazing and other land management practices. We predict that the population of *P. striatus* in OPCNM has expanded from the area occupied during the original survey for two main reasons. First, deleterious management practices have ceased, potentially allowing for increased recruitment, germination, and survival of *P. striatus* plants, as well as the regeneration of *P. striatus* nurse plants, which create suitable habitat for growth. Second, the frequency and duration of freezing temperatures in the winter has likely decreased since the population was first recorded. As winter freezing temperatures decrease, the survival and reproduction of these frost-intolerant plants might increase.

In this study, we use over 60 years of monitoring results to determine the population and habitat characteristics of *P. striatus* in OPCNM and provide some evidence of how climate and land use changes can affect succulent plants at the limits of their distributions. Our specific objectives were to: 1) determine the size, spatial distribution, and reproductive capacity of the population; 2) identify suitable habitat characteristics, including the use of nurse plants; and 3) assess past and current climate and land use threats to the population

Methods

Site Description

Organ Pipe Cactus National Monument is an International Biosphere Reserve located in southwestern Arizona, 210 km W of Tucson and 35 km S of Why, AZ (31.82–32.20°N, 112.61–113.09°W). Organ Pipe Cactus National Monument includes several high mountain ranges and low basins, with elevations ranging from 300–1470 m. Long-term (1944–2002) mean annual temperature at low elevation is 21.0°C (mean min. = 12.1°C, mean max. = 29.9°C) and mean annual precipitation (MAP) is 238 mm. Precipitation at OPCNM is bimodally distributed, with nearly half of the precipitation delivered during winter (October–March) storms and the remainder during the summer monsoon (July–September). April–June are extremely dry, with total precipitation in these months composing 4% of MAP.

Organ Pipe Cactus National Monument was established in 1937 to protect the organ pipe cactus (*Stenocereus thurberi* (Engelm.) Buxb.) and the Sonoran Desert ecosystem. The OPCNM *Peniocereus striatus* population occurs within a *Larrea tridentata-Ambrosia deltoidea* association on floodplains and lower bajadas, an *Atriplex polycarpa-A. linearis* association on loamy floodplains, and a *Prosopis velutina-Parkinsonia microphylla-Olneya tesota* association on hill slopes.

Monitoring History of the *P. striatus* Population in OPCNM

Thirty years following the first documentation of *P. striatus* in OPCNM in 1939, the National Park Service (NPS) reported the species was rare and occurred only on north- and east-facing hill slopes (Jackson 1966; Steenbergh 1966). In 1969, the (NPS) surveyed in the proximity of the original location and reported a total population of 36 plants on three hills (Goodsell unpublished). As part of the Sensitive Ecosystem Program in OPCNM, probable habitat, defined as hill slopes in the vicinity of the plants found in 1969, was surveyed for *P. striatus* in 1990. The survey resulted in the location of 59 plants (11 plants per ha in suitable habitat), which produced an estimate of the extant population in OPCNM of less than two hundred individuals (Johnson et al. 1990; Ruffner and Associates 1995). As a result of this survey, the NPS measured the height and survivorship of 22 *P. striatus* plants from 1991–1996. Another survey occurred in 1994, when 47 plants in OPCNM were located and tagged for a study on the pollination ecology of *P. striatus* (Nabhan and Suzán 1994). Some of these individuals were relocated in 1999, when volunteers surveyed the eastern portion of its range in OPCNM. Fifty-seven plants were found, tagged and mapped. About two dozen *P. striatus* plants were tagged in 1991 and revisited from 1993–1999 to determine population characteristics (Ruffner and Associates 1995), with little to no information recorded about habitat requirements.

2002 Survey

To determine the population size, distribution, and habitat preferences of *P. striatus* in OPCNM, a systematic survey was conducted from January–July 2002. Most of the survey was performed by a single person trained in the appearance and growth habits of the plant. Survey intensity ranged from belt transects (5–10 m wide) in low density vegetation to more intensive surveys in xeroriparian areas. All open areas and every nurse plant species was checked for the presence of *P. striatus*. The survey was initiated in previously occupied habitat determined by previous NPS reports (Jackson 1966; Steenbergh 1966; Goodsell unpublished) and expanded into potential habitat until the survey no longer located plants or the international boundary was encountered. Survey tracks were recorded with a high precision GPS unit (accuracy ~3 m), and survey area was created by buffering survey tracks in a GIS.

The location and elevation of *P. striatus* plants were also recorded using a high precision GPS unit. Plants were marked with numbered metal tags and the maximum height and width of each plant, as well as the number of live and dead basal stems per plant were recorded. Height and width measurements were taken during winter dormancy and only green succulent stems of plants were measured. To determine herbivory damage, the presence or absence of injury to a plant and proximity to a rodent hole were recorded. Since flower bud scars are obvious and persist for a long time, they were used to indicate reproductive status. The nurse plant (*sensu* Franco and Nobel 1989) and its spatial orientation to *P. striatus*, as well the nearest perennial plant neighbor and its distance to *P. striatus* were noted.

Slope, aspect and other descriptors of the physical environment were recorded. Soil surveys from OPCNM (USDA–Soil Conservation Service 1972) were used to produce a digital data layer of soil types within the *P. striatus* survey area. Lastly, whether or not the plant was within two meters of an ephemeral drainage was observed and recorded.

Climate and Land Use History

Precipitation was measured at the Dos Lomitas rain gauge, located within the study area, and temperature was measured at the National Weather Service station located at park headquarters 20 km NW of Dos Lomitas. To assess past land use history of the study area, a map of historic land use was prepared. A digital orthophoto quadrangle, formed from a 1997 photographic image, was used as a base layer onto which lines and polygons were drawn to indicate roads, corrals, wells, historic agricultural fields and disturbance zones. Early aerial photographs of the area were compared with the 1997 orthophoto quad to verify or interpret linear features and other patterns of land use. Some man-made features found on the ortho-photo quad were verified on the ground using GPS. Archived documents at OPCNM provided additional information on past land management activities (Rutman 1996).

Statistical Analyses

The height and width of *P. striatus* in 2002 were broken into 10 cm size classes to assess population structure. Changes in height and number of basal stems through time were evaluated using repeated measures ANOVA (R Development Core Team 2008). The proportion of the total population in each slope class, aspect, soil type, nurse plant, and nearest perennial plant was determined. Pearson's Chi-square tests were performed to determine if observed occurrences were different than an expected random distribution in potential habitat. ANOVA was also performed on height of *P. striatus* to see if there were differences among nurse plant associations. A linear regression model was fit to determine trends in temperature through time.

Results and Discussion

Population Characteristics

A survey of 172 ha of potential *Peniocereus striatus* habitat in OPCNM resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in the 1999 survey, which makes the density of the population 0.85 individuals per ha. This population size of 145 plants is larger and population density two orders of magnitude greater than estimates reported by Suzán et al. (1994). The close proximity (<3 m) of many new *P. striatus* found in the 2002 survey to those found in 1969 (Fig. 1), and the discovery of small individuals in 2002, provide further evidence that there have likely been increases in the population size. The population also appears to have expanded from its restricted spatial

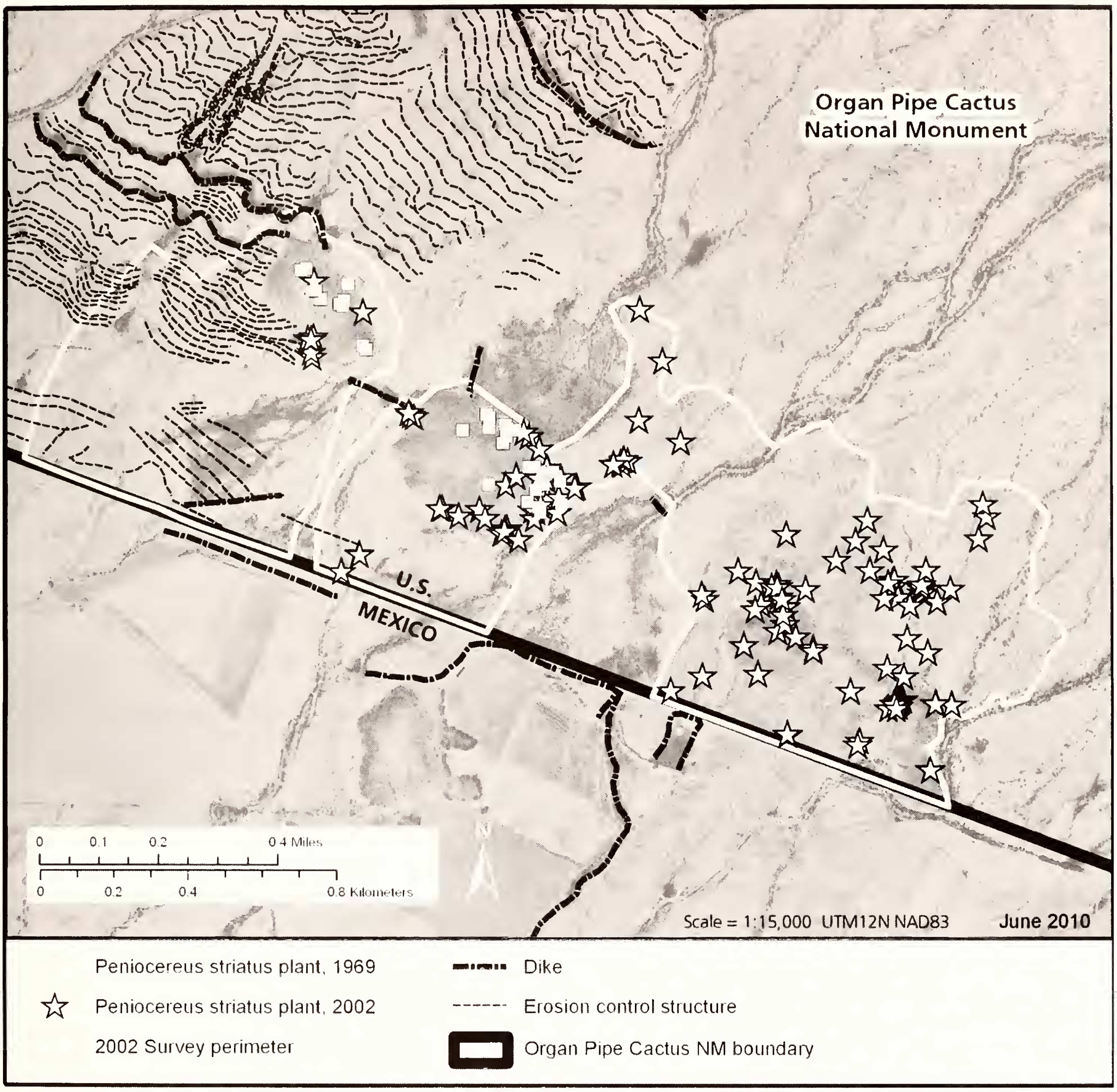

FIG. 1. Location of *Peniocereus striatus* individuals from 1969 and 2002 surveys and land use disturbances in Organ Pipe Cactus National Monument.

distribution on hillslopes in 1969 to adjacent low-lying areas, but individuals were notably absent from the farthest western portion of the survey area where intense land use modification had occurred (Fig. 1). Potential increases in population size and spatial distribution may be partially due to differences in survey efforts, which were not well described in historic records.

The mean height of plants in 1993 did not significantly change in subsequent surveys in 1994–2002 (Fig. 2a). The mean number of basal stems did not significantly change from 1999 to 2002, although there was a trend for stem number to increase (Fig. 2b). The mean height and width of plants were 58.6 cm (±2.5 cm standard error) and 54.4 cm (±3.7 cm), respectively. The height distribution of the population ranged from 1 to 158 cm and had a significant (>2 standard errors of skewness) positive skew (1.02), which means the tail of the distribution was shifted towards taller individuals (Fig. 3a). While a majority of individuals in the *P. striatus* population were 40–80 cm tall, it is likely that the interaction *P. striatus* had with nurse plants allowed for the growth of tall individuals by facilitating an environment that was favorable for plant growth. The tallest plant of 158 cm was close to the maximum recorded height of 200 cm (Felger 2000; Goodsell unpublished). The horizontal width distribution was bimodal, with most individuals <10 cm or 30–70 cm (Fig. 3b). This reflects the vine-like (narrow) and bush type

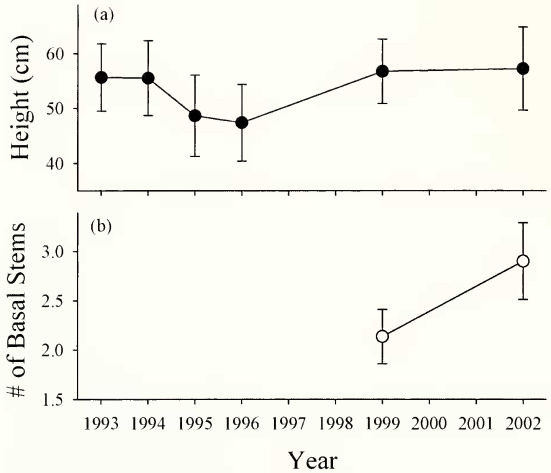

FIG. 2. Mean height (a; n = 15) and total number of basal stems per plant (b; n = 51) of *Peniocereus striatus* from 1993–2002. No significant differences among years (P > 0.05).

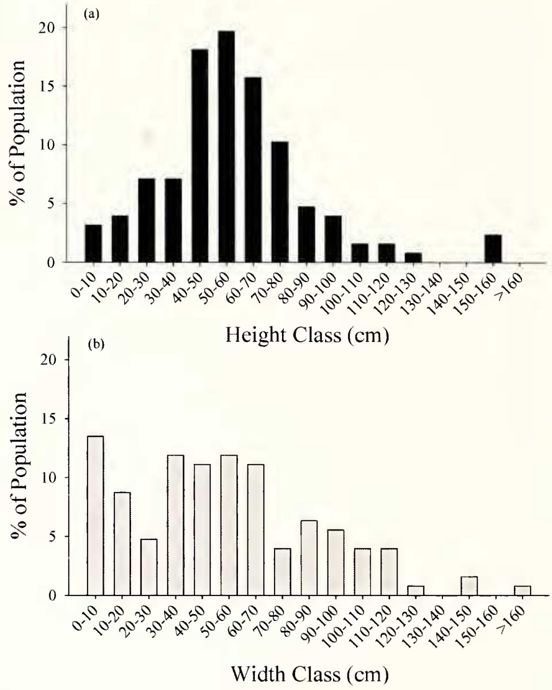

FIG. 3. Percent of the *Peniocereus striatus* population in height (a) and width (b) classes. Height distribution skewness = 1.024, kurtosis = −0.375. Skewness and kurtosis is considered significant if greater than 2 standard errors of normal distribution = ±0.436.

(wide) morphological types first described by Johnson et al. (1990). The vine-like morphs often occurred under trees and had long branches that draped across nurse plant stems, while the bush-type morphs appeared to have shorter, more erect branches and usually grew within the canopies of shrubs and subshrubs or in the open. The maximum width of 304 cm exceeded previously reported values (Johnson et al. 1990; Pinkava 1995; Anderson 2002). Most plants had a single living basal stem, although at least one plant had eight stems.

A majority of *P. striatus* individuals in the OPCNM population were sexually mature. The presence of bud scars indicated that 76% of the plants had flowered in the past. For the remainder of the population, reproductive status could not be determined, either due to herbivory or aboveground tissue damage. In July 2002, 45% of *P. striatus* individuals had buds present, including two plants that lacked bud scars from prior reproductive activity.

Habitat

Peniocereus striatus occurred at a low, fairly narrow elevation range between 388–441 m, which is within the elevation range of 60–450 m reported for this species (Benson 1982). The number of plants decreased with increasing slope: 35% of plants occurred on <2% slope, while only 5% of plants occurred on >22% slope (Table 1). This suggests that there has been expansion of the population from its restricted historical hill slope habitat. *Peniocereus striatus* occurred on every slope aspect, but had a tendency to occur less frequently on west and northwest facing slopes ($\chi^2 = 21.5$, P = 0.003, df = 7; Fig. 4a). This result is consistent with earlier reports that suggested *P. striatus* occurred less frequently on west-facing slopes (Steenbergh 1966; Goodsell unpublished). While many cacti in OPCNM attain their greatest densities on south-facing slopes since they are less subject to freezing temperatures in the winter (Parker 1987), the current *P. striatus* distribution is not limited to these slopes, perhaps because they are frequently buffered from extreme environmental conditions by nurse plants.

Peniocerius striatus occurred on five different soils and three landform types within the 2002 survey area (Table 1). Plants occurred less frequently on fine and very fine sandy loams and more frequently on rocky soils than predicted if plants were randomly distributed in their potential habitat ($\chi^2 = 109.4$, P < 0.0001, df = 5). Twenty-seven percent of the population occurred on deep, very fine or fine sandy loam on gently sloping floodplains, nearly half of the plants occurred on very gravelly or cobbly loam on dissected alluvial fans, and another quarter of the plants grew on very stony loam on hill slopes (Table 1). *Peniocerius striatus* was not found on torrifluvents of the drainage bottoms, although this substrate type only represented 4.3 percent of the survey area. Although these results are consistent with historical accounts of greater *P.*

TABLE 1. HABITAT CHARACTERISTICS OF *PENIOCEREUS STRIATUS* POPULATION AT ORGAN PIPE CACTUS NATIONAL MONUMENT.

Habitat	% of population
Slope	
0–2%	35
3–8%	25
9–14%	21
15–21%	14
>22%	5
Soil type	
Gunsight very gravelly loam	41
Gilman very fine sandy loam	26
Lomitas very stony loam	24
Harqua very cobbly loam	8
Antho fine sandy loam	1
Torrifluvents	0

striatus occurrence on rocky soils, the population has expanded to other soil types.

Nurse Plant Associations

Most *P. striatus* plants in OPCNM grew within the canopy of subshrubs, shrubs and trees. Nabhan and Suzán (1994) also found that *P. striatus* was non-randomly distributed in the environment, preferring microsites under nurse plants to microsites with no plant cover. Over half of *P. striatus* plants were nursed by shrubs and subshrubs, while 40% occurred under leguminous trees (Table 2). These results are similar to Nabhan and Suzán (1994), who found that 50% of *P. striatus* grew under trees. A majority of *P. striatus* that had nurse plants were directly within them, while most others were oriented either directly north or south of the nurse plant (χ^2 = 47.0, P < 0.0001, df = 7; Fig. 4b). An orientation north of the nurse plant can be explained by protection against excessive radiation, temperature, and water stress (Franco and Nobel 1989), while an orientation south of the nurse plant may provide protection against frost (Suzán 1994).

While we found *Prosopis velutina* Wooton to be the most commonly used nurse plant by *P. striatus*, Nabhan and Suzán (1994) reported *Olneya tesota* A. Gray was the species' principal nurse plant. Besides providing shade and physical protection, legume trees also increase soil nitrogen levels under their canopies (Franco and Nobel 1989). Johnson et al. (1990) observed that *Ambrosia deltoidea* (Torr.) W. W. Payne, *Larrea tridentata* (DC.) Coville, and *Parkinsonia microphylla* Torr. were the most common nurse plants for *P. striatus*. The earliest report of the OPCNM population mentions *Larrea tridentata* as the most common associate (Goodsell unpublished), followed in quantity by plants standing entirely alone. Nurse plant type significantly affected the

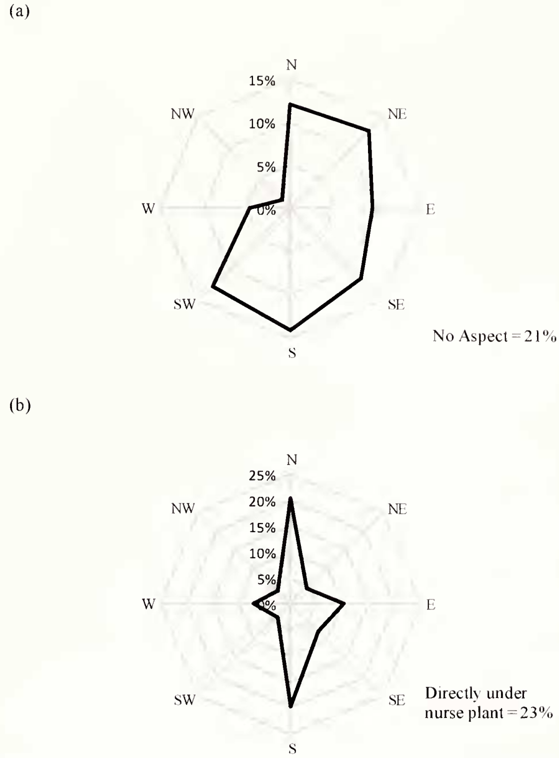

FIG. 4. Percent of the *Peniocereus striatus* population on each aspect (a) and orientation in relationship to nurse plant (b). Aspect: χ^2 = 21.4, P = 0.003, df = 7, orientation to nurse plant: χ^2 = 50.2, P < 0.0001, df = 7. Chi-square test assumes expected population is evenly distributed in each direction.

mean height of *P. striatus*. Plants underneath trees were significantly taller than those under subshrubs, while plants underneath shrubs and those with no nurse plant association had an

TABLE 2. NURSE PLANT ASSOCIATIONS OF *PENIOCEREUS STRIATUS* POPULATION AT ORGAN PIPE CACTUS NATIONAL MONUMENT.

Nurse plants	% of population
Subshrubs	25
Atriplex linearis S. Watson	13
Ambrosia deltoidea (Torr.) W. W. Payne	12
Shrubs	29
Larrea tridentata (DC.) Coville	14
Atriplex polycarpa (Torr.) S. Watson	11
Lycium spp.	4
Trees	40
Prosopis veluntina Wooton	21
Parkinsonia microphylla Torr.	12
Olneya tesota A. Gray	7
Other	6
None	4
Prosopis veluntina (dead)	1
Unknown shrub (dead)	1

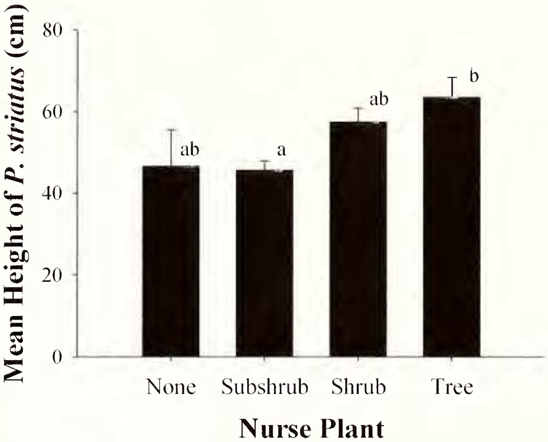

FIG. 5. Mean height of *Peniocereus striatus* in relationship to the nurse plant type (none, subshrub, shrub, tree). Different letters designate significant differences (Tukey adjusted $P < 0.05$).

intermediate height (Fig. 5). This supports our hypothesis that *P. striatus* makes opportunistic use of the structural support of the available perennial canopy and that the shrubby morph is more likely to be found in the open or under a subshrub. *Peniocereus striatus* was on average 16.7 ($\pm$1.7) cm from the nearest perennial plant, which was most commonly a subshrub (55%), either *Ambrosia deltoidea* or *Atriplex linearis* S. Watson, followed in close proximity to shrubs (30%).

Threats to Population

Climate. Most plants had at least one dead basal stem, indicating that aboveground tissue damage was widespread and common. During the winter-spring survey of 2002, 19% of *P. striatus* individuals with at least one previously green stem had all their stems become light brown, dry and brittle. Since most of the plant's biomass is belowground in diffuse tubercles (Benson 1982), this "top-kill" does not necessarily equate to plant mortality. One likely explanation for this observed "top-kill" is freezing temperatures. Temperature at the site dropped to −13.7°C on January 31, 2002, which is low enough to cause tissue damage or death of temperature-sensitive succulents (Nobel 1988). Position on the landscape significantly affected the probability of the 2002 aboveground tissue damage ($\chi^2 = 70.4$, $P < 0.0001$, df = 3): 36% of individuals that occurred ≤2 m from a drainage showed top-kill damage while only 8% of individuals >2 m from a drainage were damaged. Since drainages are frequently affected by cold nocturnal air inversions due to radiative cooling and cold air flow from sidewalls (Brunt 1939), the higher incidence of top-kill in low-lying areas was likely caused by low temperatures. By early summer 2002, more than half of top-killed plants had re-sprouted from the base or had new branches growing from the desiccated stems.

The likelihood of frost damage is likely to decrease in the future as temperatures warm due to anthropogenic greenhouse gas emissions. Over the last fifty years (1949–2002), the number of freezing days has declined from greater than 20 to less than 10 days per year (linear regression: slope = −0.33, $r^2 = 0.41$, $P < 0.0001$; Fig. 6), the average minimum January (coldest month in OPCNM) temperature has increased 2.3°C, and this average has not been below freezing since

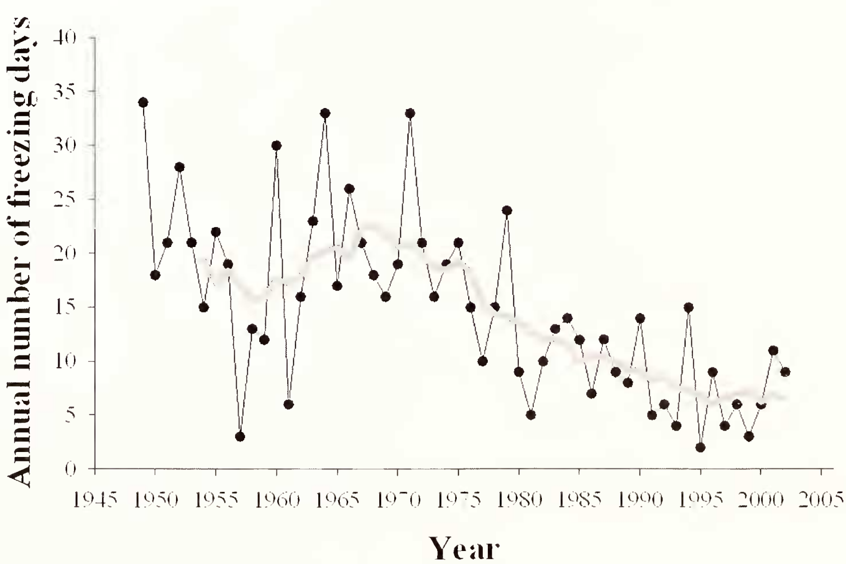

FIG. 6. Annual number of freezing days at study site from 1949–2002 (black line) and 10-year moving average (gray line). Linear regression: slope = −0.33, $r^2 = 0.41$, $P < 0.0001$.

1949 (not shown). Given that minimum temperatures likely limit the range of *P. striatus*, these changes in temperature may explain potential increases in the *P. striatus* population. Future increases in temperature are likely to result in the spread of frost-intolerant succulents and other plants northwards in their distribution.

Herbivory. Most *P. striatus* plants (70% of the population) displayed signs of herbivore damage during the winter 2002 survey, likely caused by rodents and lagomorphs. In 2002, 17% of new stems initiated in the spring showed signs of herbivory by July. Nearly half (45%) of the total population was within 1 m of a rodent hole, which suggests a high animal density in close proximity to the cactus population.

Land use. The habitat of *P. striatus* is located in an area of OPCNM heavily degraded by past land use and land management practices. Concentrated livestock grazing, wood harvesting, and farming were among the land use activities within the study site at the Gray Ranch headquarters (Rutman 1996). The overstocking of cattle had adverse environmental effects, including damage to *P. striatus* and its habitat, which continued until livestock were removed in the late 1970's (BLM 1966; Schultz et al. 1971). On certain soil types in the study area, poor livestock grazing practices led to accelerated erosion, expressed as deeply entrenched channels and headcuts that moved upstream as much as 8 m per rainstorm in 1952 (OPCNM historic photo, accession #1629). Large stumps and re-sprouted stems at the study site are signs of historic tree harvesting, while more recently, illegal woodcutters have taken tree branches using machetes (Nabhan and Suzán 1994). *Peniocereus striatus* could not have been present on a 13 acre flood-irrigated field used by the Gray family at the north end of the study area. Small diversion dams and retention dikes used to manage irrigation, which date back to the early 1930's, change water surface flows on several hundred acres of suitable habitat for *P. striatus*.

Potential habitat in the study area has also been disrupted by erosion control structures installed by the NPS and Soil Conservation Service in the 1950's–1960's. More than 50 years after their construction, these structures remained clearly visible in aerial photography (northwest corner of Fig. 1). Despite these structures, erosion rates have not slowed since 1977 (T. Marsh, unpublished data, 1977–1996). The loss of soil has undoubtedly had consequences for the local *P. striatus* population, as the roots would have been exposed or buried, depending on landscape position. *Peniocereus striatus* has not been found in or adjacent to these erosion control structures, which suggests that the species may be sensitive to the local watershed modifications caused by these structures.

Previous surveys and knowledge about the study area's land use history provides some evidence that the *P. striatus* population was historically restricted to rocky hill slope habitat, as reported by early surveyors. This landscape position was largely left undisturbed by livestock grazing, erosion, agriculture, and watershed modifications, which were concentrated on the low-lying and flatter portions of the landscape. The cessation of livestock grazing, coupled with warmer temperatures, may have allowed for the expansion of *P. striatus* into areas of the landscape where it was previously not found. Erosion control structures and their long-term effect on hydrology continue to exclude this species from otherwise suitable habitat.

Acknowledgments

This work was supported by a grant from the USGS Status and Trends of Biological Resources Program. We wish to thank NPS and the Arizona-Sonora Desert Museum for their support and encouragement for this project. We are grateful to Tom Van Devender and Ana Lilia Reina, who showed G.A. *Peniocereus striatus* in Mexico, Peter Holm, who provided climate data, and Andy Hubbard for his input. Thanks to Kathleen Parker, Mary Moran, and two anonymous reviewers for helpful suggestions on how to improve earlier versions of this paper. Any use of trade, product, or firm names in this paper is for descriptive purposes only and does not imply endorsement by the U.S. Government. All authors contributed equally to this work. In memory of NPS Ranger Kris Eggle, 1973–2002.

Literature Cited

Anderson, E. 2002. The cactus family. Timber Press, Portland, OR.

Benson, L. 1950. The cacti of Arizona, 2nd ed. University of New Mexico Press, Albuquerque, NM.

———. 1982. The cacti of the United States and Canada. Stanford University Press, Stanford, CA.

Brunt, D. 1939. Physical and dynamical meteorology, 2nd ed. Cambridge University Press, Cambridge, U.K.

Bureau of Land Management (BLM). 1966, Forage resource inventory of the Organ Pipe Cactus National Monument–narrative report for the National Park Service. BLM–Arizona State Office, Phoenix, AZ.

Felger, R. S. 2000. Flora of the Gran Desierto and the Rio Colorado of northwestern Mexico. University of Arizona Press, Tucson, AZ.

Franco, A. C. and P. S. Nobel. 1989. Effect of nurse plants on the microhabitat and growth of cacti. Journal of Ecology 77:870–886.

Hastings, J. R. 1963. Historical change in the vegetation of a desert region. Ph.D. dissertation, University of Arizona, Tucson, AZ.

Jackson, V. L. 1966. Memorandum to the superintendent, chief naturalist's monthly narrative report. Unpublished report, archives file A2615, Organ Pipe Cactus National Monument. Ajo, AZ.

Johnson, R. A., M. A. Baker, D. J. Pinkava, N. Trushell, and G. A. Ruffner. 1990. Special status plants of Organ Pipe Cactus National Monument, AZ, Sensitive Ecosystems Project, Final Report. Organ Pipe Cactus National Monument, Ajo, AZ.

Lyford, M. E., S. T. Jackson, J. L. Betancourt, and S. T. Gray. 2003. Influence of landscape structure and climate variability on a Late Holocene plant migration. Ecological Monographs 73:567–583.

Malcolm, J. R., C. Liu, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology 20:538–548.

Nabhan, G. P. 1992. Status survey of *Peniocereus greggii* and *P. striatus* in the Sonoran Desert. Contract report for U.S. Fish and Wildlife Service, Albuquerque, NM.

——— and H. Suzán. 1994. Boundary effects on endangered cacti and their nurse plants in and near a Sonoran Desert biosphere reserve. Occasional Papers in Conservation Biology 1:55–67.

Nobel, P. S. 1988. Environmental biology of agaves and cacti. Cambridge University Press, Cambridge, U.K.

Parker, K. C. 1987. Site-related demographic patterns of organ pipe cactus populations in southern Arizona. Bulletin of the Torrey Botanical Club 114:149–155.

Pinkava, D. J. 1995. Cactaceae, pt. 1, The ceroid cacti. Journal of the Arizona-Nevada Academy of Science 29:9–10.

R Development Core Team. 2008, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, Website: http://www.r-project.org/ [accessed 12 December 2010].

Rabinowitz, D. 1981. Seven forms of rarity. Pp. 205–217 *in* H. Synge (ed.), The biological aspects of rare plant conservation. John Wiley and Sons, New York, NY.

Raguso, R. A., C. Henzel, S. L. Buchmann, and G. P. Nabhan. 2003. Trumpet flowers of the Sonoran Desert: floral biology of *Peniocerius* cacti and Sacred *Datura*. International Journal of Plant Science 164:877–892.

Ruffner and Associates. 1995. Organ Pipe Cactus National Monument ecological monitoring program monitoring protocol manual, Special Report No. 11, National Biological Service-Cooperative Park Studies Unit, University of Arizona, Tucson, AZ.

Rutman, S. 1996. Livestock grazing and accelerated erosion on Organ Pipe Cactus National Monument, Ajo, AZ. Organ Pipe Cactus National Monument, Ajo, AZ.

Schultz, R. L., E. L. Webb, J. P. Townsend, and W. K. Carter. 1971. Range conditions on the Organ Pipe Cactus National Monument–a special study for the National Park Service. Bureau of Land Management, Arizona State Office, Phoenix, AZ.

Shreve, F. 1911. The influence of low temperatures on the distribution of the giant cactus. Plant World 14:136–146.

Steenbergh, W. F. 1966. Memorandum to the Superintendent, unpublished report, 1 May 1966. Organ Pipe Cactus National Monument, Ajo, AZ.

Suzán, H., G. P. Nabhan, and D. T. Patten. 1994. Nurse plant and floral biology of a rare night blooming Cereus *Peniocereus straitus* (Brandegee) F. Buxbaum. Conservation Biology 8:461–470.

———, ———, and ———. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. Journal of Vegetation Science 7:635–644.

U.S. Department of Agriculture (USDA)–Soil Conservation Service. 1972, Soil survey–a special report: Organ Pipe Cactus National Monument, Pima County, Arizona. Soil Conservation Service, Phoenix, AZ.